

POST-DISPERSAL SEED PREDATION VARIES BY HABITAT NOT ACORN SIZE FOR *QUERCUS CHRYSOLEPIS* (FAGACEAE) AND *LITHOCARPUS DENSIFLORA* (FAGACEAE) IN CENTRAL COASTAL CALIFORNIA

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ABSTRACT

In this study, I investigated the effects of seed size and habitat on post-dispersal predation of *Quercus chrysolepis* and *Lithocarpus densiflora* acorns in central coastal California. Tagged acorns were located at five distances across two forest-grassland ecotone sites. Although *Q. chrysolepis* acorns were nearly twice as large as those of *L. densiflora*, there was no significant difference in predation between the species or sites. There was, however, a significant difference in acorn predation between habitats, with both species having much higher rates of predation in the forest than in the grassland. While predation occurred across the forest-grassland ecotone, acorn burial only occurred in the forest. These results suggest that habitat had a stronger effect on post-dispersal predation than seed size.

Key Words: forest-grassland ecotone, seed dispersal, seed predation, seed size, *Quercus chrysolepis*, *Lithocarpus densiflora*.

Seed predation can have a large impact on plant distributions and abundances (Crawley 1992). Among the many factors that affect seed predation, the habitat where seeds are located after they are dispersed can play a significant role in determining the amount of predation (Louda 1989). Early work predicted that predation would decline with increasing distance from parent trees (Janzen 1970), and this pattern has been generally confirmed in a range of different habitats (e.g., Cintra 1997; Manson et al. 1998). In addition to variation within habitats, other studies have shown that seed predation may also vary among adjacent habitats (Maron and Simms 1997; Hubbard and McPherson 1999; Nystrand and Granstrom 2000) and at range of spatial (Louda 1982; Sousa and Mitchell 1999) and temporal (Maron and Simms 1997) scales.

A second factor believed to play an important role in seed predation is seed size (Thompson 1987). Theoretically, seeds with larger energy reserves should provide a greater energy return to seed predators and therefore have higher predation than small seeds. While a number of intra-specific and inter-specific studies have documented that larger seeds are consumed more frequently than smaller seeds (Kelrick et al. 1986; Reader 1993; Moegenberg 1996), other work suggests that seed size may not directly affect seed predation (Geritz 1998; Sousa et al. 2003).

Species in the family Fagaceae have been the focus of many post-dispersal predation studies because their typically large seeds are dispersed and consumed by animals (Van der Wall 2001). Rates of seed predation in the genus *Quercus* have been shown to vary across habitats (Kikuzawa 1988; Quintana-Ascencio et al. 1992; Hubbard and McPherson 1999), but no studies have compared how

post-dispersal predation is affected by habitat and seed size. As part of a larger study of the factors affecting woody plant establishment across the forest-grassland ecotone, I investigated the role of seed size and habitat on post-dispersal predation of acorns of *Quercus chrysolepis* Liebm. and *Lithocarpus densiflora* (Hook. & Arn.) Rehder. My specific research objectives were 1) to determine the independent and interactive effects of acorn size and habitat on rates of post-dispersal acorn predation and 2) to better understand how the observed patterns in post-dispersal predation may influence woody plant establishment across forest-grassland ecotones.

METHODS

Study Area

The study was conducted along Bolinas ridge in the Marin Municipal Water District watershed on Mount Tamalpais (37°54'N, 122°37'W) in southern Marin County, CA. The mixed evergreen study forests contain *Pseudotsuga menziesii* (Mirbel) Franco *L. densiflora* (hereafter *Lithocarpus*), *Quercus agrifolia* Nee, *Q. chrysolepis* (hereafter *Quercus*), *Arbutus menziesii* Pursh, *Umbellularia californica* (Hook. & Arn.) Nut., and *Sequoia sempervirens* (D. Don) Endl. (Horton et al. 1999). The grasslands are a mixture of exotic annuals and native and exotic perennials (J. Corbin personal communication). The study area is characterized by a mediterranean climate with seasonal summer dry period and average annual precipitation of 1250 mm (Dunne and Parker 1999).

Quercus and *Lithocarpus* acorns fall most heavily between late September and early November (P. Kennedy personal observation). Both are primarily

small-mammal and bird dispersed (Van der Wall 2001). The western grey squirrel (*Sciurus griseus*) is the primary disperser in the study area, although the Steller's jay (*Cyanocitta stelleri*) may also move acorns (P. Kennedy personal observation). Primary post-dispersal acorn predators include the aforementioned dispersers, acorn woodpeckers (*Melanerpes formicivorus*), mule deer (*Odocoileus Hemionus*), and gophers (*Thomomys* spp.).

Experimental Design

In October 2002, *Quercus* and *Lithocarpus* acorns were collected from a number of trees along Bolinas ridge. The acorns were brought back to the laboratory, immersed in water, and all those still floating after five minutes were considerable inviable and removed (Nyandia and McPherson 1992). Viable acorns were surface sterilized in a 10% bleach solution for five minutes, air dried, and stored at 4°C for a week before tagging. A subset of the acorns of both species was weighed prior to storage ($n = 123/\text{species}$). The acorn tagging method was modified from Forget et al. (1998). A 1-mm diameter hole was drilled through the center of the acorns and threaded with a 1-m piece of fishing line. The line was double-knotted on both sides of the acorn, and a small numbered tag made of orange flagging tape was attached to the opposite end of the line. A pilot study showed that tagging had no effect on seed handling by dispersers/predators (P. Kennedy unpublished data).

Two sites (C and D) separated by approximately 1 km were randomly selected for the seed predation experiment. At both sites, five distances across the forest-grassland ecotone were located: far grassland (20 m into the grassland), near grassland (5 m into the grassland), edge (at the forest-grassland ecotone edge), near forest (5 m into the forest), and far forest (20 m into the forest). At each distance, a 50-m transect running parallel to the forest-grassland ecotone was delineated. Along each transect, 12 one-m² plots, separated by least one m, were randomly established. Each plot was randomly assigned either *Quercus* or *Lithocarpus* acorns ($n = 60$ plots/species). Within each plot, eight acorns were randomly located on the soil surface ($n = 480$ acorns/species: two sites \times five distances \times six plots/distance). The acorns were placed in the plots on October 15. On November 15, the 100-m² area within and around each plot was visually surveyed for ~5 minutes/plot by three people, and the number of acorns and/or tags remaining was recorded.

Statistical Analyses

Acorn weights of *Quercus* and *Lithocarpus* were compared using a Welch's two-sample t-test. An F-test revealed that the variances were heterogeneous; however, the data were normally distributed. To quantify acorn predation, acorns were scored as

"handled" or not. I defined handled as acorns that were eaten, buried, moved, or missing. Although some of the buried, moved, or missing acorns may have escaped predation, the number of moved and missing acorns was low, and many studies have shown that the majority of buried acorns are eventually eaten (see Van der Wall 2001). Therefore, I consider handling to be a maximum estimate of predation. Acorn handling was analyzed using a three-way mixed model ANOVA, with species and distance as fixed factors and site as a random factor. Prior to analysis the data was arcsine transformed to homogenize variances (Cochran's C test, $P > 0.01$). A Tukey HSD test was used for an *a posteriori* comparison between means. Due to low sample sizes and heterogeneous variances, the proportions of acorns eaten and buried were not analyzed statistically.

RESULTS

Acorn size varied significantly between *Quercus* and *Lithocarpus*, with *Quercus* acorns were almost twice as large as those of *Lithocarpus* (*Quercus*: 7.48 ± 0.15 g (mean \pm standard error), *Lithocarpus*: 4.73 ± 0.09 g; $t = 15.13$, $df = 199$, $P < 0.001$). Despite this difference, the amount of acorn handling did not vary significantly between species (species: $F_{1,1} = 3.75$, $P = 0.305$) or sites (site: $F_{1,100} = 0.85$, $P = 0.36$). However, acorn handling did vary across the forest-grassland ecotone (distance: $F_{1,4} = 378.28$, $P < 0.001$). For both species, acorn handling was significantly higher in the forest than the grassland, while the edge experienced intermediate levels of handling (Fig. 1). There were no significant higher-order interactions (species \times site: $F_{1,4} = 2.69$, $P = 0.18$; species \times distance: $F_{4,100} = 0.65$, $P = 0.63$; site \times distance: $F_{1,4} = 2.02$, $P = 0.26$; species \times site \times distance: $F_{4,100} = 0.12$, $P = 0.98$).

For both *Quercus* and *Lithocarpus*, the proportion of acorns eaten in the forest was much higher than in the grassland and intermediate at the edge (Table 1). While there were some acorns eaten in the grassland, no acorns were buried in that habitat. In the forest, *Lithocarpus* had somewhat higher rates of burial than *Quercus*, being highest in the near forest at site D. At all distances, the proportion of acorn eaten was always higher than the proportion buried across species.

DISCUSSION

Although *Quercus* acorns were nearly twice as large as those of *Lithocarpus*, post-dispersal predation did not vary by seed size, but rather by habitat. Both species were consistently handled, eaten, and buried more often in the forest than in the grassland. Patterns of higher acorn predation in forests have been observed in previous studies of *Quercus*. Kikuzawa (1988) found that *Q. mongolica* acorns disappeared fastest from areas with in-

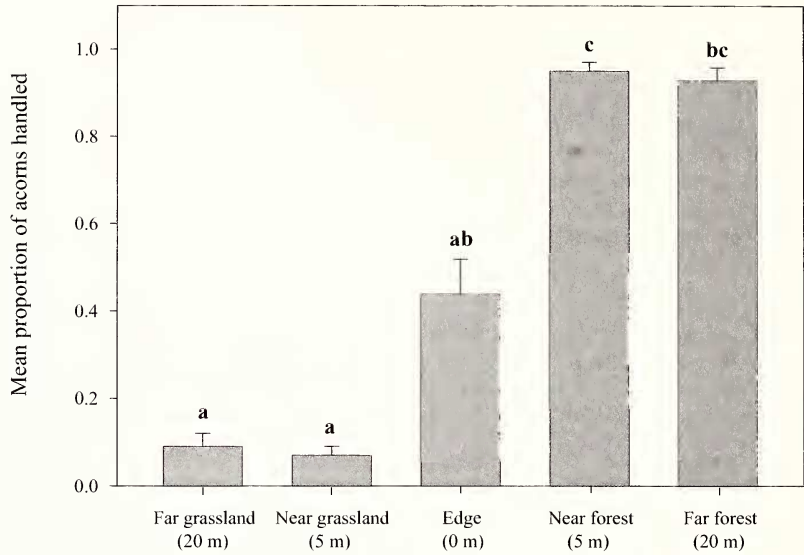


FIG. 1. Mean (\pm one SE) acorn handling of *Quercus chrysolepis* and *Lithocarpus densiflora* across the forest-grassland ecotone on Mt. Tamalpais, CA in 2002. Different letters indicate significant differences among distances ($P = 0.05$). See text for definition of acorn handling.

tact forest canopy and slowest from adjacent bare areas. Similarly, Hubbard and McPherson (1999) documented that predation of *Q. emeryi* acorns was 50% higher under intact canopies than in adjacent grasslands; however, the presence or absence of understory vegetation had no effect on acorn predation in areas with intact canopies. The relatively rapid loss of acorns in the forest (83–96% after one month) was also comparable to rates seen elsewhere. Kikuzawa (1988) showed that after four days all the *Q. mongolica* acorns in unenclosed intact forest locations had been removed. Miyaki and

Kikuzawa (1988) observed the rate of acorn disappearance between fall and winter to be 49% and 99% by the following spring. Similarly, in an eastern U.S. deciduous forest, Sork (1984) found that seed predators consumed greater than 99% of the *Q. rubra* acorns in an eight month period.

While there were a significantly greater number of acorns eaten in the forest than in the grassland, there were also a larger number of acorns buried in the forest as well. Buried acorns often have much higher survival rates than unburied acorns (Borchert et al. 1989; Fuchs et al. 2000), and the absence

TABLE 1. MEAN PROPORTIONS OF ACORNS EATEN AND BURIED ACROSS TWO FOREST-GRASSLAND ECOTONE SITES ON MOUNT TAMALPAIS IN 2002. Standard errors are given in parentheses.

	Far Grassland (20 m)	Near Grassland (5 m)	Edge (0 m)	Near forest (5 m)	Far forest (20 m)
Proportion eaten					
<i>Quercus</i>					
Site C	0 (0)	0.17 (0.06)	0.52 (0.18)	0.94 (0.04)	0.98 (0.02)
Site D	0.02 (0.02)	0.02 (0.02)	0.50 (0.16)	0.98 (0.02)	0.98 (0.02)
<i>Lithocarpus</i>					
Site C	0.15 (0.05)	0.11 (0.05)	0.44 (0.19)	0.96 (0.03)	0.94 (0.04)
Site D	0.13 (0.08)	0 (0)	0.31 (0.15)	0.94 (0.04)	0.83 (0.11)
Proportion buried					
<i>Quercus</i>					
Site C	0 (0)	0 (0)	0 (0)	0.07 (0.03)	0.09 (0.05)
Site D	0 (0)	0 (0)	0 (0)	0.13 (0.00)	0.05 (0.03)
<i>Lithocarpus</i>					
Site C	0 (0)	0 (0)	0 (0)	0.09 (0.04)	0.23 (0.11)
Site D	0 (0)	0 (0)	0 (0)	0.53 (0.07)	0.36 (0.09)

of observed acorn burial in the grassland may limit the rate of successful oak establishment in that habitat. Johnson et al. (1997) found that jays preferentially buried nuts in forest and edge habitats over open grassland habitats; however, others have putatively observed acorn burial by jays in fields (Deen and Hodges 1991). While some studies demonstrate that small mammals do transport acorns into grasslands (Stapanian and Smith 1986; Kollman and Schill 1996), many others have shown that small mammals visit non-forested areas less frequently due to increased risk of mortality by predation (Kikuzawa 1988; Miyaki and Kikuzawa 1988; Quintana-Ascencio et al. 1992; Van der Wall 2001). At both study sites, large raptors were frequently seen flying near the forest-grassland ecotone, which may dissuade small mammals from moving acorns in the grassland.

The reasons why site D had higher proportions of acorn burial than site C and *Lithocarpus* acorns were buried more frequently than those of *Quercus* are less clear. Site D had a slightly more open understory than site C, which may have influenced the dispersers' handling of the acorns. Alternatively, small mammal densities may have varied between sites, which could also have altered handling decisions. Both sites had acorn producing *Lithocarpus* individuals in the canopy, and although they appeared to be qualitatively similar in background acorn density, there may have been slight differences in acorn quantities as well.

Preferences for specific species of seeds have been observed in many small mammal feeding studies (Smith and Follmer 1972; Fox 1982; Jacobs 1992). Lewis (1982) found that squirrel selection of acorns from different species varied according to the energy return of the acorn. The *Quercus* acorns in this study presumably had greater energy return than *Lithocarpus* acorns based on their larger size, which may partially explain their higher proportions of consumption relative to burial at both sites. However, the chemical composition (e.g., tannin levels) of the acorns may also have varied between species, which could have affected the patterns of consumption and burial as well (Smallwood and Peters 1986). One explanation for the relatively high levels of predation of both *Quercus* and *Lithocarpus* may be due to germination strategy. Acorns that do not have a dormant phase are often at least partially consumed immediately by small mammals to decrease acorn loss to seedling germination (Fox 1982). Both Hadj-Chikh et al. (1996) and Smallwood et al. (1998) found that squirrels and other caching animals effectively discriminated between red (which have a dormant phase) and white (which do not have a dormant phase) oak acorns. Since neither *Lithocarpus* nor the *Quercus* species in this study exhibits a dormant phase this may contribute to the high consumption for both species.

In conclusion, I found that habitat plays a more

significant role in post-dispersal acorn predation than seed size. Variation in acorn handling across the forest-grassland ecotone may have important implications for seedling establishment. Very high rates of acorn predation in the forest suggest that seedling recruitment there may be seed limited; however, masting, which is common among oaks and can satiate seed predators, may allow some seedlings to establish regardless of high levels of predation. Furthermore, higher rates of seed burial in the forest will also facilitate greater establishment in that habitat relative to the adjacent grasslands. Post-dispersal acorn predation is clearly affected by a wide range of ecological factors and additional studies are needed to identify other influences controlling this phenomenon. Specifically, studies that determine the chemical composition and nutritional quality of the acorns of both species will help resolve questions about handling decisions. In addition, observational studies of the dispersers will better illuminate the role of habitat in acorn predation. Finally, studies examining a wider range of seed sizes within and between species will provide greater support for the effect of seed size of acorn predation.

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